

Article

Seasonal Variability in Present-Day Coccolithophore Fluxes in Deep Eastern Mediterranean Sea: A Multi-Year Study (2015–2017) of Coccolithophore Export in SE Ionian Sea at 4300 m Depth

Sikandar Hayat ^{1,2} , Elisavet Skampa ¹ , Alexandra Gogou ³, Spyros Stavrakakis ³, Constantine Parinos ³ and Maria Triantaphyllou ^{1,*} 

¹ Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimioupolis, 15784 Athens, Greece

² Department of Earth Sciences, University of Lille 1, Cité Scientifique, CEDEX, 59655 Villeneuve d'Ascq, France

³ Institute of Oceanography, Hellenic Centre for Marine Research, P.O. Box 712, 19013 Anavyssos, Greece

* Correspondence: mtriant@geol.uoa.gr

Abstract: This study is the first attempt to understand the coccolith flux and its seasonal variability at the deepest part of the Mediterranean Sea. Samples were obtained from the deepest Mediterranean time-series sediment trap (4300 m) moored in the SE Ionian Sea (Nestor site) from January 2015 to November 2017. Throughout the study period, the coccolith fluxes displayed a seasonality signal with high values during the late winter–early spring convective mixing period (February to April) and low flux values during summer except for some solitary peaks in June. The maximum coccolith flux was observed in March 2015 while the minimum value was recorded in November 2017. Among the nineteen identified species of heterococcoliths, the dominant species in all the samples was *Emiliania huxleyi* reaching up to 79%, followed by *Florisphaera profunda* that comprised up to 33% of the total coccolith count. For the annual cycle of 2015, the average coccolith flux for the Nestor Site at a relatively shallower depth (2000 m) was comparable and for some time intervals was lower than the coccolith flux recorded in the present study at 4300 m, while coccolith flux peaks appeared simultaneously in both traps indicating a fast sinking rate. The higher *E. huxleyi*, *F. profunda*, *Gladiolithus flabellatus*, and *Calciosolenia brasiliensis* coccolith flux at 4300 m compared with their corresponding fluxes at 2000 m can be attributed to lateral advection, resuspension, and/or the influence of Eastern Mediterranean Deep Waters (EMDWs).

Keywords: coccolith flux; Eastern Mediterranean; biogenic flux; Ionian Sea; sediment trap; *Emiliania huxleyi*; *Florisphaera profunda*



Citation: Hayat, S.; Skampa, E.; Gogou, A.; Stavrakakis, S.; Parinos, C.; Triantaphyllou, M. Seasonal Variability in Present-Day Coccolithophore Fluxes in Deep Eastern Mediterranean Sea: A Multi-Year Study (2015–2017) of Coccolithophore Export in SE Ionian Sea at 4300 m Depth. *J. Mar. Sci. Eng.* **2022**, *10*, 1761. <https://doi.org/10.3390/jmse10111761>

Academic Editors: Antoni Calafat and Weidong Zhai

Received: 14 September 2022

Accepted: 12 November 2022

Published: 16 November 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Coccolithophores are a group of unicellular calcifying marine algae that dwell in the photic zone and cover their cells with an exoskeleton (coccosphere) comprised of tiny calcite platelets (1–20 µm across) called coccoliths [1]. They account only for 1–10% of marine primary productivity (PP); however, they exert a key influence on the ocean chemistry as they utilize CO₂ via photosynthesis to produce particulate organic carbon (POC) (carbon pump), as well as release CO₂ during the production of coccoliths/particulate inorganic carbon (PIC) (counter carbon pump) [2]. The flux of CO₂ between the photic zone of the ocean and the atmosphere is mainly dependent on PIC to POC ratio [2,3]; thus, the production of coccolithophore blooms results in an increase in the CO₂ content of the ocean on a short timescale. Due to the high density of calcite, coccoliths act as ballasts and expedite the removal of POC out of the surface waters [4,5]. Coccolithophores are expected to adapt better than other phytoplankton groups, e.g., diatoms, to the nutrient

limitation that is expected due to enhanced stratification of the water column because of rising global temperatures [6,7]. Their assemblage composition is sensitive to seasonal changes and mirrors the oceanographic and environmental conditions of the photic zone. Hence, coccolithophore fluxes transfer the ecological signals of the photic zone to deep water and seafloor sediments [8].

Coccolithophores are the dominant phytoplankton group in the Eastern Mediterranean constituting a major portion of settling biogenic particles with pronounced seasonal variations [9–13]. Earlier sediment trap studies in the area have shown seasonal and interannual fluctuations in coccolithophore fluxes in response to changing sea surface temperature (SST), nutrient availability, and precipitation; maxima were observed during the winter–spring mixing period [8,13–16]. Occasional high fluxes have been recorded during summer, driven by short-lived events, e.g., atmospheric input, or upward movement of nutrient-rich intermediate waters [13]. The species *Emiliania huxleyi* dominates the upper photic zone, while *Florisphaera profunda* thrives in the deeper layers [17,18].

Nestor site is located in the SE Ionian Sea, the deepest basin of the Mediterranean (between 4600 and 5264 m depth) [12]. Hence, the Nestor sediment trap deployment at five successive depths, with the deepest sediment trap moored at 4300 m [12], offers a unique opportunity to study downward fluxes and document coccolithophore export fluxes at the deepest part of the Eastern Mediterranean water column. Previous time series studies at the Nestor site have focused on the downward fluxes of the major geochemical components investigating the mechanisms of vertical transport from 700 m down to 4300 m depth during 2006–2010 [12], whereas the analysis of coccolithophore fluxes has been restricted only to 2000 m depth for the time interval 2010–2015 [13]. This study presents, for the first time, the analysis of coccolithophore export fluxes from the deepest basin of the Mediterranean Sea. Thus, the aim of the present study is to analyze the deepest sediment trap samples acquired from Nestor site, in order to (a) quantify the coccolithophore primary productivity fluxes at 4300 m during the 2015–2017 time interval, (b) investigate the assemblage composition and detect the signal of surface seasonality signal in the deep water masses, and (c) compare the obtained coccolithophore fluxes with data of previous studies from different depths at Nestor site to determine potential alterations in the sinking coccolithophore assemblages.

Oceanographic Setting

Even though the semi-enclosed water body of the Mediterranean Sea covers only 0.8% of the global ocean, it has comparable features, particularly thermohaline circulation, complex bathymetry, and deep water convection [19]. Nestor site (Figure 1) is located in the Eastern Mediterranean near the SW Peloponnese peninsula in the SE Ionian Sea. The SE Ionian Sea, which contains the deepest basins of the Mediterranean Sea, has complex morphology with steep slopes, plateaus, and valleys [12]. Terrestrial input is negligible as there is no riverine inflow in the area [20]. The slopes are almost bare and the valley/basin floor contains thin layers of pelagic sediments indicating the absence of turbidity flow [12]. Sea surface temperature (SST) ranges from 15.1 °C to 29.3 °C where May–October are warm and November–April are cold months with the highest precipitation in the colder period [13]. The surface chlorophyll concentrations are highest during the late winter–early spring convective mixing period, lowest during the summer months [21], generally remaining below 0.5 mg L^{−1} in the open sea [22,23]. During winter and spring, the combined effect of the two westerly upper air jet streams namely the polar front jet stream and the subtropical jet stream, result in the east–southeast propagation of subtropical cyclones which outcomes in the fertilization of Mediterranean water by Saharan dust [24], while most of the atmospheric deposition in the Mediterranean Sea occurs as wet deposition [25].

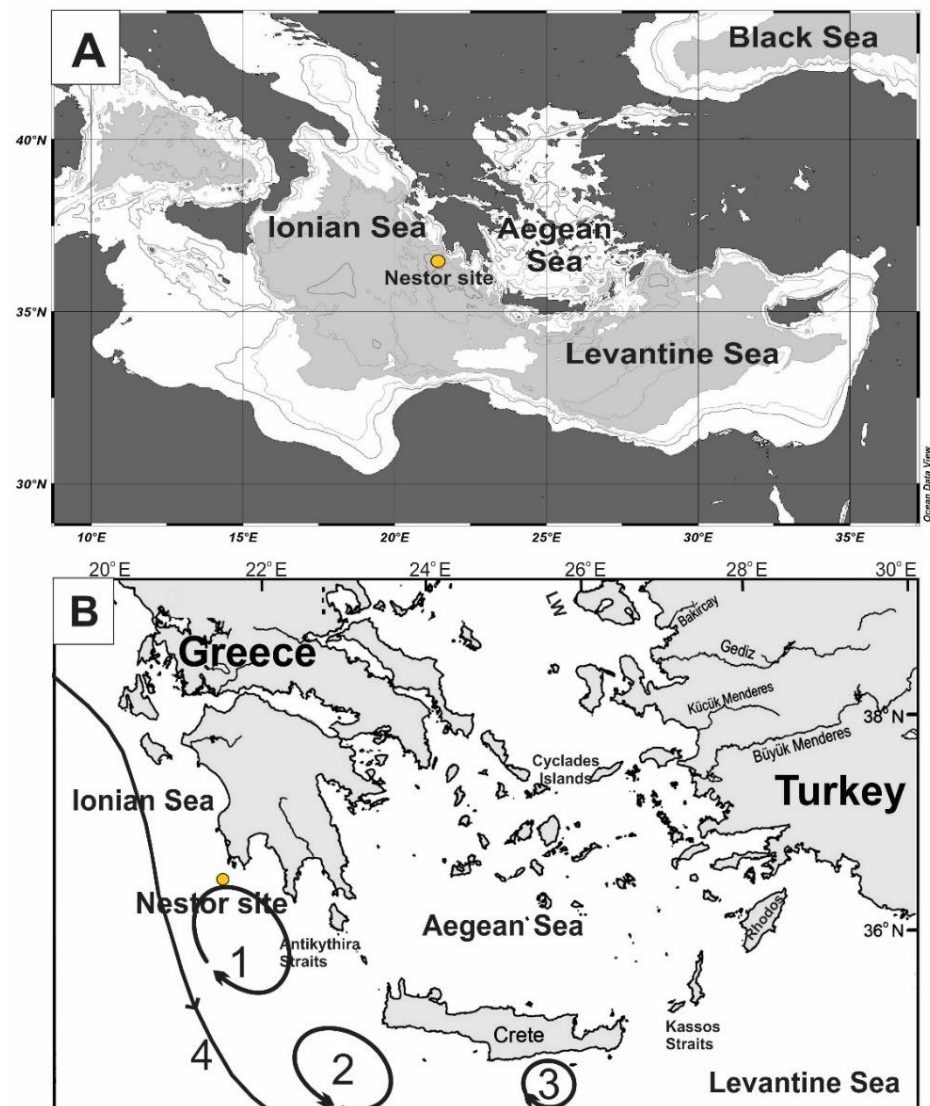


Figure 1. (A). Location of sampling site (Nestor site) in the SE Ionian Sea (Eastern Mediterranean Sea), (B). General circulation pattern in top 500 m (1. Pelops anticyclone, 2. Cretan cyclone, 3. Ierapetra anticyclone, 4. Atlantic–Ionian stream).

Eastern Mediterranean surface waters are P-starved due to the anti-estuarine circulation, atmospheric input from Sahara with high N/P (100:1), and limited denitrification [26,27]. The oligotrophic signature of the Ionian Sea is evident from the 80–100 m Deep Chlorophyll Maximum (DCM), which shows low seasonality [28].

Modified Atlantic Water (MAW), Levantine Intermediate Water (LIW), the Transitional Waters, and Eastern Mediterranean Deep Water (EMDW) are the four major water masses of the Ionian Sea from the surface downwards.

With temperature and salinity of 17.4 °C, 38.72 psu (25–100 m water depth); 15 °C, 39 psu (100–500 m water depth); 13.8 °C, 38.76 psu (500–1200 m water depth), and 13 °C, 38.6 psu (>1200 m water depth), respectively [29,30]. Nestor site is located at the edge of Pelops anticyclone, which disperses the intermediate waters that enter the Ionian Sea through southern Crete to the south, north, and west [31]. Pelops anticyclone was observed to turn off or weaken during summer, which results in the upward movement of intermediate waters [32].

2. Materials and Methods

2.1. Satellite Environmental Data

The satellite data (chlorophyll-a (Chl-a), Precipitation, and SST) were obtained from EarthData-Giovanni open access database (<http://disc.sci.gsfc.nasa.gov/giovanni/> accessed on 11 October 2022) [33]. An average of 8 days of data was obtained for satellite Chl-a concentration from MODIS-Aqua (MODerate resolution imaging spectroradiometer) (4 Km resolution) through the National Aeronautic and Space Administration (NASA) Giovanni website (<http://disc.sci.gsfc.nasa.gov/techlab/giovanni/> accessed on 11 October 2022) for the following boxes. The coordinates of satellite data for Chl-a and SST are 36.2292–36.5625° N, 21.2292–21.5625° E and for precipitation: 36.375–36.375° N, 21.375–21.375° E.

2.2. Deployment and Recovery of the Sediment Trap Mooring

PPS3/3 Technicap sediment trap (0.125 m² collecting area) was deployed at 4300 m depth from January 2015 to November 2017, at the Nestor site (36°2.96' N, 21°28.93' E) by the Hellenic Centre for Marine Research (HCMR; R/V Aegaeo, project KRIPIS), with a number of time gaps (see Table 1). After recovery, samples were stored in the dark at 4 °C until further processing. To remove large organisms, samples were sieved through 1 mm nylon sieve whereas swimmers smaller than 1 mm were removed under the light microscope using tweezers. Afterward, each sample was divided into subsamples using a high-precision peristaltic dispensing pump.

Table 1. Time intervals and sample codes of the analyzed sediment trap samples.

2015		2016		2017	
Sample Code	Sampling Date	Sample Code	Sampling Date	Sample Code	Sampling Date
KMS XV 7	16–31 January 2015	KMS XVII 8	16–31 March 2016	KMS XVIII 2	1–31 May 2017
KMS XV 8	1–15 February 2015	KMS XVII 9	1–15 April 2016	KMS XVIII 3	1–30 June 2017
KMS XV 9	16–28 February 2015	KMS XVII 10	16–30 April 2016	KMS XVIII 4	1–31 July 2017
KMS XV 10	1–15 March 2015	KMSXVII 11	1–15 May 2016	KMS XVIII 5	1–31 August 2017
KMS XV 11	16–31 March 2015	KMS XVII 12	16–31 May 2016	KMSXVIII 6	1–30 September 2017
KMS XV 12	1–15 April 2015	No data (1 June 2016 to 30 April 2017)		KMSXVIII 7	1–31 October 2017
No data (16 April to 31 May 2015)				KMS XVIII 8	1–30 November 2017
KMS XVIII 8	1–30 November 2017				
KMS XVI 1	1–15 June 2015				
KMS XVI 2	16–30 June 2015				
KMS XVI 3	1–15 July 2015				
No data (16 July to 15 August 2015)					
KMS XVI 6	16–31 August 2015				
KMS XVI 7	1–15 September 2015				
KMS XVI 8	16–30 September 2015				
KMS XVI 9	1–15 October 2015				
KMS XVI 10	16–31 October 2015				
No data (1 November 2015 to 15 March 2016)					

2.3. Sample Preparation

Each subsample was first split into 10 equal fractions by McLane rotary wet splitter (<4% deviation between aliquots). One fraction of each subsample was processed in ultrasonic for two minutes to disintegrate pellets and aggregates, then further subdivided with the rotary splitter, and necessary sub-fractions depending upon the coccolith density of samples were filtered onto Millipore cellulose acetate filter (diameter: 47 mm; pore size: 0.45 µm) using a vacuum pump. Afterward, the filter was put in the oven (40 °C) for 30 min to dry and then stored in petri dishes. The solution used in the process of splitting was pre-distilled water that was buffered with sodium carbonate (pH > 8). A small random

triangular portion of the filter (approx. 30 mm²) was mounted on a glass slide for the microscopic analysis.

2.4. Quantitative Microscopic Analysis

For the coccolithophore analysis, we followed standard sample preparation and light microscopy techniques of previous sediment trap studies in the Eastern Mediterranean, e.g., [8,13–16] to ensure the accuracy of data comparison.

The quantitative analysis of coccolith assemblages was performed using Zeiss AxioScope 5 polarizing light microscope at the magnification of 1000×. Coccolith counting for each sample was performed in a filter area of 2 mm², except for *E. huxleyi* which was counted in the first 1 mm² area. The list of identified species is shown in Table 2. The total coccolith flux and each species' coccolith flux were calculated using the equation of Ziveri et al. [34]: $F = (N \times Af \times S) / (af \times Ast \times T)$, where F = coccolith flux (coccolith m⁻² day⁻¹), N = number of counted coccoliths, Af = effective filtration area (mm²), S = split factor, af = investigated filtration area (mm²), Ast = sediment trap aperture area (m²), T = duration of sampling (days).

Table 2. List of coccolithophore species recorded in the studied sediment trap samples.

<i>Algirosphaera robusta</i> (Lohmann, 1902) Norris, 1984
<i>Calcidiscus leptoporus</i> (Murray and Blackman, 1898) Loeblich and Tappan, 1978
<i>Calciosolenia brasiliensis</i> (Lohmann, 1919) Young, 2003
<i>Ceratolithus cristatus</i> Kamptner, 1950
<i>Coccolithus pelagicus</i> (Wallich, 1877) Schiller, 1930 subsp. <i>pelagicus</i>
<i>Discosphaera tubifera</i> (Murray and Blackman, 1898) Ostenfeld 1900
<i>Emiliania huxleyi</i> (Lohmann, 1902) Hay and Mohler in Hay et al. 1967
<i>Florisphaera profunda</i> Okada and Honjo, 1973
<i>Gephyrocapsa oceanica</i> Kamptner, 1943
<i>Gladiolithus flabellatus</i> (Halldal and Markali, 1955) Jordan and Chamberlain, 1993
<i>Helicosphaera carteri</i> (Wallich, 1877) Kamptner, 1954
<i>Pontosphaera</i> spp.
<i>Rhabdosphaera clavigera</i> Murray and Blackman, 1898
<i>Scyphosphaera</i> spp.
<i>Syracosphaera mediterranea</i> Lohmann 1902
<i>Syracosphaera pulchra</i> Lohmann, 1902
<i>Umbellosphaera tenuis</i> (Kamptner, 1954) Paasche, 1955
<i>Umbilicosphaera sibogae</i> (Weber-van Bosse, 1901) Gaarder, 1970

3. Results

3.1. Satellite Measurements of Surface Chl-A Concentration, SST, and Precipitation

Satellite measurements of surface Chl-a concentration (Figure 2) displayed a seasonal pattern with the highest values occurring during late winter–spring (max.: February 2015; 0.2 µg L⁻¹; Figure 2). The annual cycle can be subdivided into a warm (May–October) and a cold season (November–April) according to the SST with values ranging from 15.3 to 29.5 °C, whereas the precipitation followed an anticorrelating pattern with the rainy season maxima during late winter–spring and increased precipitation interval beginning with distinct events within the fall of each annual cycle (Figure 2).

3.2. Total Coccolith Flux

The total coccolith flux at Nestor site at 4300 m ranged from 3.63×10^8 coccoliths m⁻² day⁻¹ (late February 2015) to 0.06×10^8 coccoliths m⁻² day⁻¹ (November 2017) (Figure 3). Despite the existence of several sampling gaps, the total coccolithophore fluxes displayed an overall uniform seasonal pattern with higher values from February to April and lower values for the rest of the year, except for some solitary peaks during summer (Figure 3). In particular, high

coccolith flux was observed from February to March 2015, with an additional single peak in June (3.5×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$). For 2016, the highest coccolith flux was recorded in early April (1.37×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$) in contrast to 2017, when the highest flux was observed in June (3.57×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$).

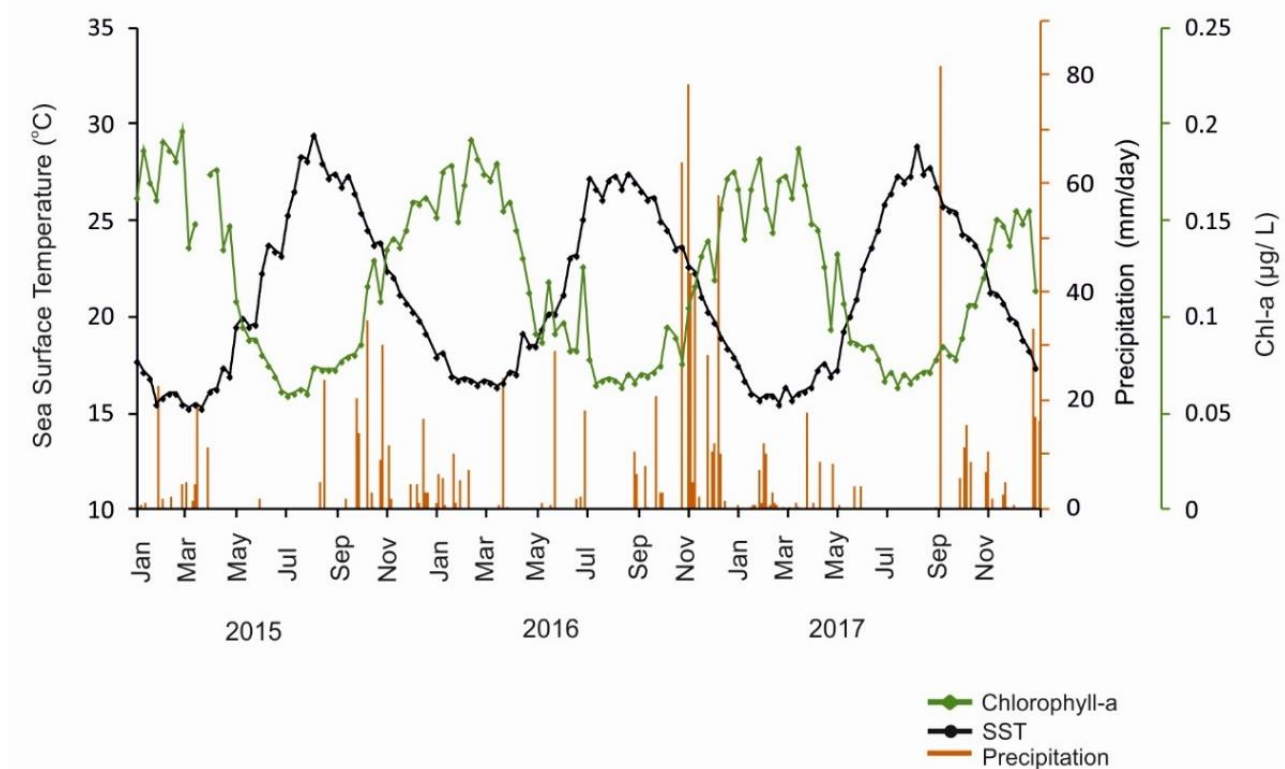


Figure 2. Satellite-derived data of the study area's SST, chlorophyll-a, and precipitation variations during the studied time interval. (Obtained from <http://disc.sci.gsfc.nasa.gov/techlab/giovanni/> accessed on 11 October 2022) (all analyses of this study were produced with the Giovanni online data system that is developed and maintained by the NASA GES DISC).

3.3. Coccolithophore Assemblage Composition

In total 19 species of heterococcoliths were identified in the studied samples (see Table 2). *Emiliania huxleyi* was the dominant species (Figure 3), reaching maxima in coccolith flux and relative abundance during early March 2015 (2.4×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$, 77%) and June 2017 (2.39×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$, 67%). The second-most abundant species was *F. profunda* (9–33 %) with maximum coccolith flux recorded in June 2017 (0.9×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), late February 2015 (0.73×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), and early June 2015 (0.59×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), while the highest relative abundance of the species was recorded in July 2017 (33 %). Other species that contributed significantly (max 5–8%) to total coccolith flux included *S. pulchra* (max. late February 2015: 0.2×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), *U. sibogae* (max. late June 2015: 0.28×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), *R. clavigera* (max. late February 2015: 0.2×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), *G. flabellatus* (max. late February 2015: 0.2×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), and *C. brasiliensis* (max. late February 2015: 0.16×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$). Finally, *Calcidiscus leptoporus* and *Helicosphaera carteri* (both up to 2%), displayed their maxima in June 2017 (0.06×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$) and February 2015 (0.03×10^8 coccoliths $\text{m}^{-2} \text{day}^{-1}$), respectively.

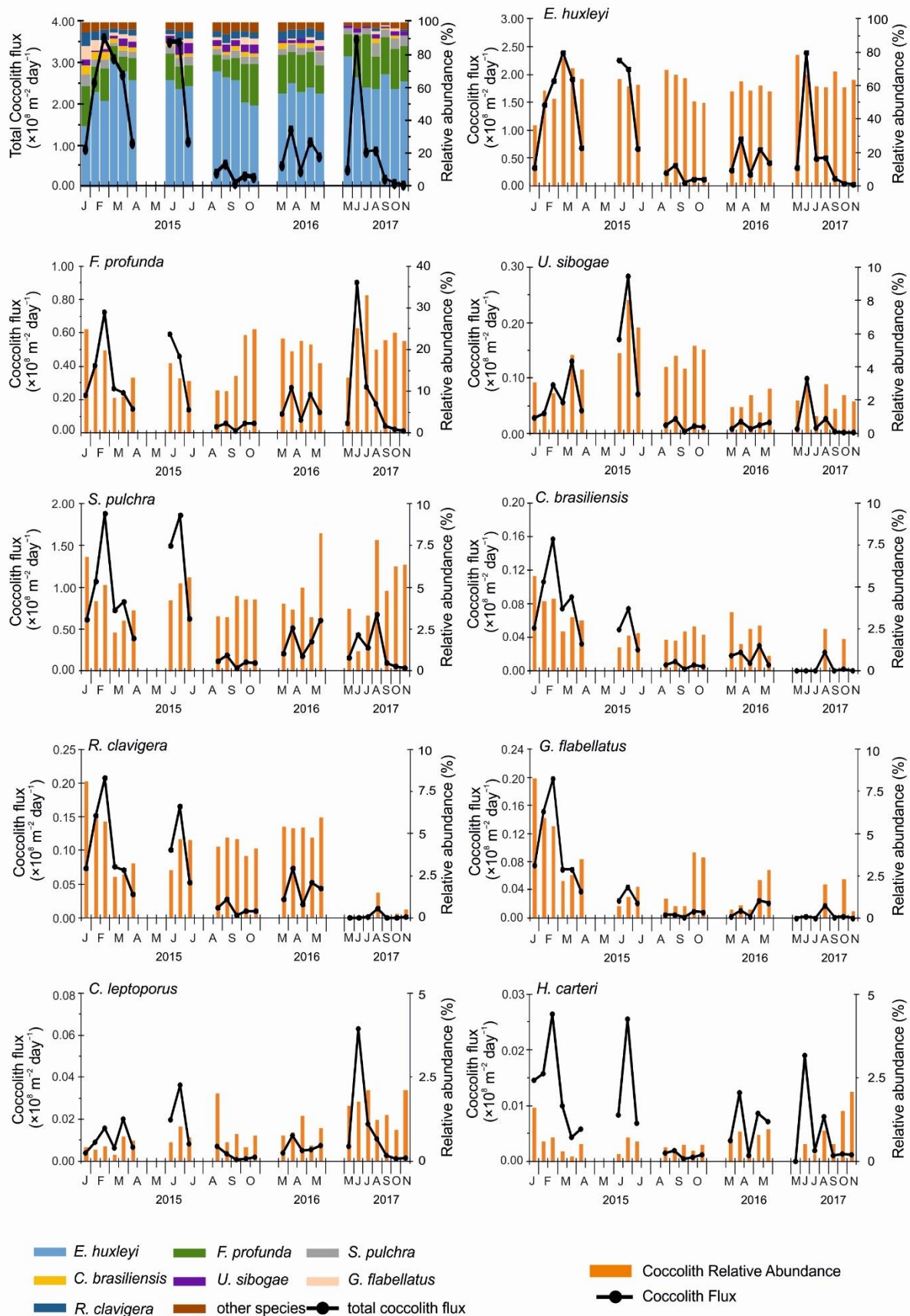


Figure 3. Total coccolith flux and major species coccolith fluxes and relative abundances recorded at 4300 m at Nestor site, SE Ionian Sea.

4. Discussion

4.1. Total Coccolith Flux and Seasonal Trends of Major Coccolithophore Species

Throughout the study period, the coccolith flux at 4300 m displayed a seasonality signal following sea surface productivity, with high values during the late winter–early spring converting mixing period (February to March; Figure 3), when the water column stratification breaks down providing nutrients to the photic zone and enhancing PP [8,12–15,35,36]. Similarly, Stavrakakis et al. [12] detected a peak in total mass fluxes in the late winter/early spring interval, coinciding with relative increases in organic carbon (OC) and opal fluxes at all investigated depths. These seasonal flux maxima were attributed by Stavrakakis et al. [12] to the development of siliceous and nannophytoplankton blooms in the euphotic zone, as also verified by our findings. The coccolith flux peaks at 4300 m depth are well-associated with increased Chl-a values, precipitation events (Figure 2), and increase in atmospheric dust input [24] that contributes significantly to fertilize the Mediterranean surface waters [13,14]. Secondary high isolated peaks were observed during summer and fall time intervals (June 2015, September 2015, June–August 2017; Figure 3), reflecting occasional high productivity in the summer months that is linked to nutrient intrusion due to the upwelling of high salinity CIW and/or LIW water masses [12,13]. This upwelling can be attributed to the seasonal pattern of Pelops anticyclone (Nestor Site is located at the edge of Pelops anticyclone, Figure 1) that repeatedly weakens or totally disappears in the summer months [32]. Likewise, Gogou et al. [37] attributed a similar isolated PP peak during June–July 2012 to the intrusion of LIW/CIW intermediate waters. In agreement with the summer peaks recorded in the present study, Stavrakakis et al. [12] noticed a pronounced flux maximum in all biogenic (OC, carbonate, and opal) fluxes in late spring/summer (May–July) of each year. During this interval, the lithogenic fluxes were also considerably high, indicating enhanced lithogenic inputs in the marine environment as a result of aeolian transport, as supported by Stavrakakis et al. [12].

The coccolith flux signal of all the major species followed the same pattern as of the total coccolith flux; with the highest values documented during high productivity seasons, as also revealed by the increased Chl-a values (Figures 2 and 3). In addition, during the late winter–early spring high productivity season, the conditions are favorable for zooplankton, thus production of pellets increases, which expedites the sinking of coccolithophores [24,38]. Alternatively, high productivity is linked to high input of Saharan dust that fertilizes the surface waters [12,13] but also acts as a ballasting mechanism [39] and can explain the simultaneous increase in fluxes. Skampa et al. [13] reported a significant increase in lithogenic fluxes during the winter–spring high coccolithophore productivity period in the Ionian Sea associated with prominent dust events. Dust is high over the Mediterranean Sea throughout the year but most of the dust deposition (65–80%) occurs as wet deposition during colder months [40] triggering the formation of large aggregates and expediting the sinking process [41]. Hence, it seems rather possible that pellets and dust are both acting as ballast during the spring peak in the SE Ionian, facilitating fluxes down to 4300 m depth, while the high abundance of coccoliths due to the productivity peak is also the reason to expedite the overall flux of both coccoliths and ballast [42]. As shown in previous studies [13–15], the total mass, total coccolith, and total CaCO_3 fluxes were reported to increase simultaneously, implying the above-described driving mechanisms. In contrast, during summer the high water column stratification in the Eastern Mediterranean hampers vertical transport, while the upwelling of intermediate waters mostly causes the observed productivity and the subsequent increase in grazer's pellets is primarily responsible for the ballasting. However, isolated precipitation events coupled with slight productivity increase (e.g., June 2016, June 2017; Figure 2) may also have expedited the sinking process, resulting in sporadic flux peaks in summer.

The major species observed at the 4300 m depth are comparable to those detected in other shallower Eastern Mediterranean sites [8,10,13–18]. The coccolith assemblage was dominated by *E. huxleyi* with species' relative abundance ranging from 38 to 79% (practically above 50 %, except for January 2015; Figure 3). The species dominance was also observed in other deep eastern Mediterranean sites, e.g., at 500 m (up to 85%) and 1700 m

depth in the Cretan Basin [15] and at 3000 m depth in the Bannock Basin (up to 95%) [14], linked to the phosphate-limited conditions of the eastern basin [15], under which *E. huxleyi* thrives [43].

The relative abundance of the intermediate and deep photic zone (DPZ) species *C. brasiliensis* (0–5.6%), *F. profunda* (9–33%), and *G. flabellatus* (0–8.3%) followed the same seasonal pattern (Figure 3). The year-round presence of DPZ species supports the constant presence of Deep Chlorophyll Maximum (DCM) in the SE Ionian Sea [8]. *Florisphaera profunda*, which represented the second-most abundant species in the assemblages (9–33%), has been widely used to understand the changes in nutricline depth in stratified, oligotrophic waters [40,44,45]. The species' constant presence has been previously observed in other sites of the SE Ionian Sea at 500 m and 2800 m (average 23 and 35%, respectively) [8] and at 500 m and 1700 m depth in the Cretan Basin (average 9%) [15]. Except for the high PP interval, the DPZ species were observed to maintain more or less the same relative abundances annually (Figure 3), which indicates their capacity to endure to the summer stratified water column and deep nutricline. However, high relative abundance for all three species was observed during the pre-high PP period in January 2015. In addition, the high relative abundance of *F. profunda* and *C. brasiliensis* was recorded during the pre-high PP interval of March 2016. The prominent pre-high PP abundance of DPZ species can be explained alternatively by two processes. During December–February, the mixed layer is deep but nutrients slowly start to penetrate the lower photic zone, which facilitates the increase in DPZ species, while as the mixing of water column increases during spring, *E. huxleyi* starts to dominate the assemblages [16]. The alternative explanation for high DPZ species relative abundance in January–February can be the influence of atmospheric triggers and surface water circulation patterns that creates turbidity, reducing the penetration of light and forcing DPZ species to move upwards to shallower depths [46], where they can benefit from nutrient availability, e.g., via wet dust deposition.

The highest peak of *S. pulchra* coccolith flux was observed during February and June 2015 (high productivity seasons). Similar to the findings of the Cretan basin (average *S. pulchra* coccolith relative abundance 3.32%, [15]), the species high relative abundance was recorded in our study for the high SST months (average 5%, max 8%) (Figures 2 and 3), showing its affinity to stratified and oligotrophic waters as well as to higher nutrient availability [14,16]. *Rabdosphaera clavigera* followed the same trend as *S. pulchra*, with the highest flux in February 2015; however, for the sampling period of 2017 it is completely absent, except for August 2017 where it contributes to the assemblages but much less compared with *S. pulchra*. *Umbilicosphaera sibogae*, which prefers warm, stratified, oligotrophic waters and displays a negative correlation to upwelling [47], and showed the highest relative abundance during the summer (June to October 2015), coinciding with the high SST-low precipitation period (Figures 2 and 3).

Helicosphaera carteri flux was overall low and makes up less than 1% of total coccolith flux for most of the year, which confirms the oligotrophic character of the study site [10,48]. The species' coccolith flux was highest during the high PP interval of early February 2015, while it also showed high values during the rest of the high productivity intervals, confirming its correlation with an increase in nutrient availability and PP [15,18]. Likewise, previous studies at southwestern margin of Crete [16] have shown that *H. carteri* (average 2.6%) dominated over the *Helicosphaera* species, with highest values recorded during the late winter to spring high flux period. At the present study, its' high relative abundance was observed during the pre-mixing period (January 2015) and in the post-high PP interval (September to November 2017), which either indicates its tolerance for a variety of trophic conditions or suggests high input of freshwater via precipitation [49–51].

4.2. Comparison of Coccolith Fluxes at 2000 m and 4300 m for the 2015 Sampling Interval

For the better understanding of the coccolithophore fluxes in the deep Ionian Sea we performed comparisons with previous studies in the area [13], concerning a single annual cycle (2015) when there is a time overlap of the available data. Skampa et al. [13] studied

the coccolithophore export flux at the Nestor site at 2000 m depth from 2010 to 2015. The sampling interval of 2015 overlaps with the time period of the present study; therefore, the comparison of coccolith fluxes at 2000 m and 4300 m would contribute to understanding the coccolith flux dynamics in the Ionian Sea water column (Figure 4). Skampa et al. [13] documented the peak season of coccolithophore flux at 2000 m in between February to March 2015, reflecting the sea surface productivity. The second peak in coccolith flux at 2000 m was observed in June 2015 (Figure 4), while the major contributors were *E. huxleyi* (30–87%) and *F. profunda* with the secondary presence of *S. pulchra*, *R. clavigera*, *A. robusta*, *S. mediterranea*, and *U. sibogae* with the peak fluxes of all major species occurring simultaneously with the total coccolith flux. The first coccolithophore flux maxima at 2000 m coincided with the time of convective mixing during the late winter–spring transition [13], while for the summer peak the intrusion of LIW/CIW intermediate water triggered by dry and cold northerly winds was considered responsible based on a similar observation in 2012 by Gogou et al. [37].

The comparison of the total coccolith and the major contributing species' fluxes at 2000 m obtained by Skampa et al. [13] with their fluxes at 4300 m recorded in the present study (Figures 4 and 5), reveals that the coccolith flux is comparable between the two depths with flux peaks appearing almost instantaneously. In particular, the total coccolith flux correlation between 2000 m and 4300 m during 2015, showed a statistically significant common monthly pattern between the two studied depths ($R^2 = 0.92$ and $p < 0.0005$; Figure 5). The period of peak productivity at 4300 m was from February to March, which coincided with the peak productivity at 2000 m (Figure 4), with both traps deployed within the EMDW water mass, thus suggesting fast sinking particle velocities in the deep Ionian Sea water column.

Interestingly, the peak fluxes of *E. huxleyi*, *R. clavigera*, and the DPZ species *F. profunda*, *G. flabellatus*, and *C. brasiliensis* were higher at 4300 m (Figure 4). This may be attributed to their increased contribution to the total coccolith flux during the recorded peaks, as well as to their dissolution tolerance. In contrast, *U. sibogae*, *S. pulchra*, *H. carteri*, *C. leptoporus*, and other minor species presented higher fluxes at 2000 m [13], possibly implying that these taxa are dissolution prone and cannot fully survive the sinking process up to 4300 m. Overall, the total coccolith flux was higher at 4300 m during February and June 2015, i.e., the highest flux periods; in addition to the increased PP, the vertical sinking mechanism and aggregate formation are triggered during these intervals, adding to fast transfer of the coccoliths to deeper layers of the Ionian water column.

The comparison between the export fluxes at 2000 m [13] and 4300 m (present study), shows that apart from export production from the photic zone resuspension or lateral inputs occasionally enhanced the coccolith fluxes at 4300 m, as the sediment trap is located near the sea bottom (4500 m). Similarly, Stavrakakis et al. [12] observed enhanced total fluxes at 4300 m depth and ascribed them to the influence of resuspension and lateral advection from the slope margin. Higher coccolith fluxes of *E. huxleyi* and *F. profunda* (Figure 4) at 4300 m, supports the impact of the above-mentioned bottom processes that alters the coccolithophore export flux signal of the photic zone in the Ionian Sea.

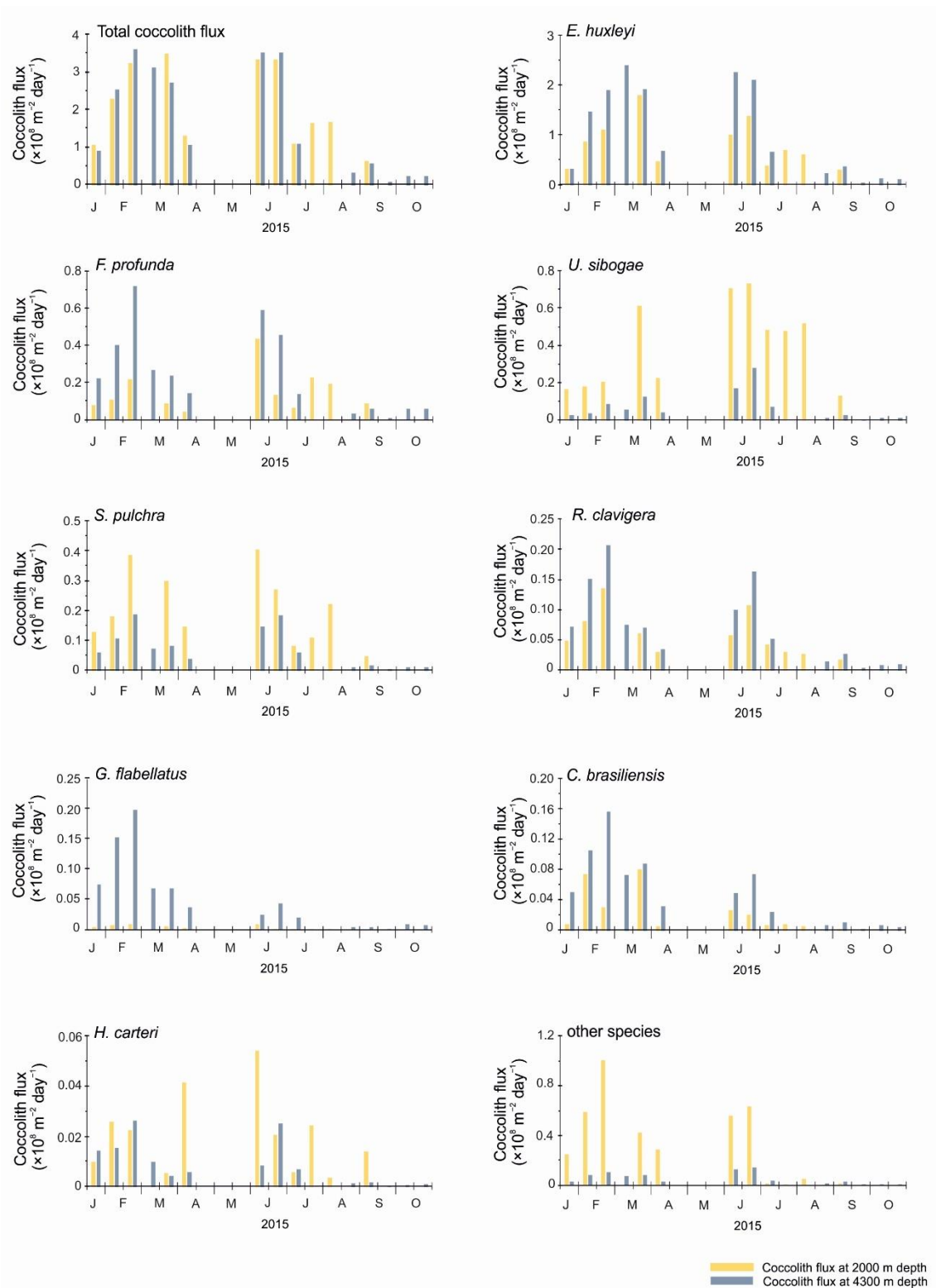


Figure 4. Comparison of the total and major species coccolith fluxes recorded at 2000 m [13] with their fluxes at 4300 m during the 2015 annual cycle sampling interval at Nestor site (2000 m [13] and 4300 m, present study). The total and major species coccosphere units from 2000 m depth (data from Skampa et al. [13]) were converted to coccoliths following the method by Boeckel and Baumann (2008) [52] and were incorporated to the coccolith fluxes at 2000 m depth.

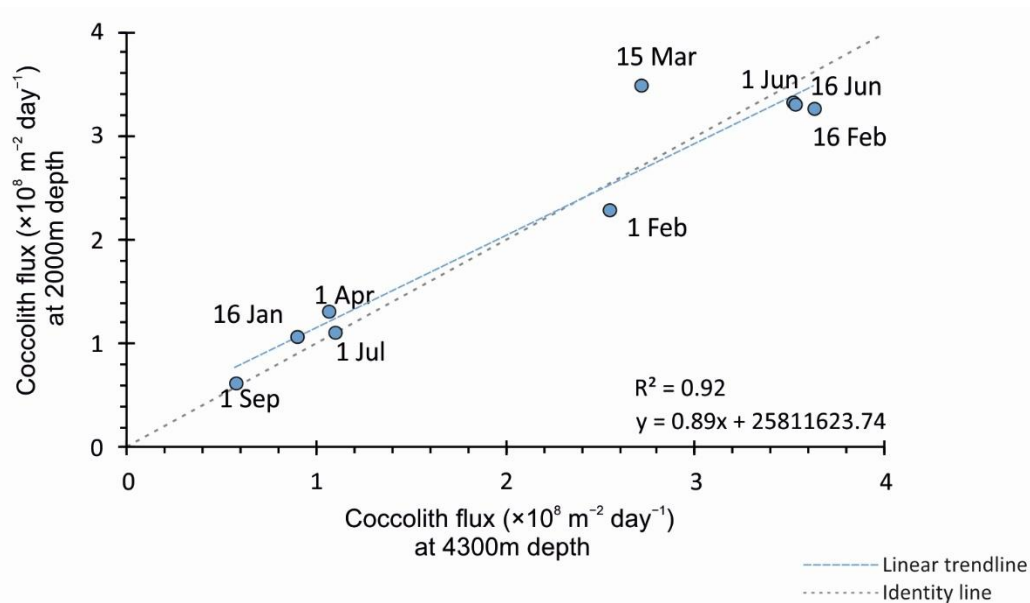


Figure 5. Correlation of the total coccolith fluxes recorded at 2000 m by Skampa et al. [13] with their fluxes at 4300 m during 2015 recorded in the present study.

5. Conclusions

The current study provides important insight into the seasonal variability, environmental control, and quantification of coccolithophore export fluxes at the Nestor site, located in the deepest basin of the Mediterranean. The coccolith flux in the studied sediment trap (4300 m), the deepest of the deployment, was documented and analyzed for the time interval of 2015–2017. In all the studied samples, a high abundance and diversity of coccoliths were observed. The results of the present study were compared with the coccolithophore flux data from 2000 m water depth, reported by Skampa et al. [13]. The main conclusions are described below:

Coccolith fluxes followed a seasonal pattern with the highest values during February–March 2015 (max 3.63×10^8 coccoliths $\text{m}^{-2} \text{ day}^{-1}$) followed by June 2017 (max 3.57×10^8 coccoliths $\text{m}^{-2} \text{ day}^{-1}$). The coccolith flux peak during the winter–spring transition period was attributed to convective mixing, while summer peaks were potentially linked to the weakening of Pelops anticyclone and the simultaneous nutrients increase due to regional upwelling. Our findings suggest fast downward particle velocities and preservation of the sea surface seasonal pattern within the Eastern Mediterranean/Ionian Sea deep water column.

In total 19 species of heterococcolithophores were identified. *Emiliania huxleyi* dominated the assemblage (38–79%), indicating the P-limited conditions of the Ionian Sea. The second-most abundant species was *E. profunda* (9–33%) and its significant presence points to the year-round presence of DCM in the study area. Other species that contributed significantly to the coccolith flux were *G. flabellatus*, *S. pulchra*, *C. brasiliensis*, *R. clavigera*, and *U. sibogae*. The assemblage composition was comparable to other shallower E. Mediterranean sediment trap sites, further verifying the preservation of the euphotic zone productivity signal at the deep Nestor site.

The comparison with coccolith flux at 2000 m for the 2015 sampling interval showed that flux at 4300 m was similar and in some cases even higher, possibly due to the influence of resuspension and lateral advection. Nevertheless, the high flux peaks were observed almost instantaneously at both depths pointing to the fast transfer within the deeper layers of the Ionian Sea water column, further enhanced by wet dust deposition and the associated aggregate formation that accelerated the sinking processes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse10111761/s1>, File S1: Major and minor species coccolith relative abundance in Nestor Site sediment trap (4300 m), File S2: Satellite Measurements of Surface Chl-A Concentration, SST, and Precipitation.

Author Contributions: Conceptualization, S.H., E.S., and M.T.; methodology, S.H., and E.S.; validation, A.G., S.S., and C.P.; writing—original draft preparation, S.H.; writing—review and editing, M.T., E.S., and A.G.; visualization, S.H.; supervision, M.T.; project administration, M.T. All authors have read and agreed to the published version of the manuscript.

Funding: This research is partly supported by Erasmus+ programme of European Union through the scholarship awarded to Sikandar Hayat by PANGAEA consortium (<https://master-pangea.eu/>; “European Joint Master in Paleontology, Geoconservation, Applications”, 2019–2025; Erasmus Mundus Joint Master Degree Project Number—610506-EPP-1-2019-1-FR-EPPKA1-JMD-MOB) for his joint master’s degree education at University of Lille and National and Kapodistrian University of Athens. This research was funded by the Greek National Project CLIMPACT: Flagship Initiative for Climate Change and its Impact by the Hellenic Network of Agencies for Climate Impact Mitigation and Adaptation.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data supporting reported results can be found in the Supplementary Materials (Files S1 and S2).

Conflicts of Interest: The authors declare no conflict of interest.

References

- Piñaar, R.N. Ultrastructure and calcification of coccolithophores. In *Coccolithophores*; Winter, A., Siesser, W.G., Eds.; Cambridge University Press: Cambridge, UK, 1994; pp. 13–38.
- Rost, B.; Riebesell, U. Coccolithophores and the biological pump: Responses to environmental changes. In *Coccolithophores*; Thierstein, H.R., Young, J.R., Eds.; Springer: Berlin/Heidelberg, Germany, 2004; pp. 99–125. [\[CrossRef\]](#)
- Cermeño, P.; Dutkiewicz, S.; Harris, R.P.; Follows, M.; Schofield, O.; Falkowski, P.G. The role of nutricline depth in regulating the ocean carbon cycle. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 20344–20349. [\[CrossRef\]](#) [\[PubMed\]](#)
- Armstrong, R.A.; Lee, C.; Hedges, J.I.; Honjo, S.; Wakeham, S.G. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2001**, *49*, 219–236. [\[CrossRef\]](#)
- Ziveri, P.; de Bernardi, B.; Baumann, K.H.; Stoll, H.M.; Mortyn, P.G. Sinking of coccolith carbonate and potential contribution to organic carbon ballasting in the deep ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2007**, *54*, 659–675. [\[CrossRef\]](#)
- Šupraha, L.; Gerecht, A.C.; Probert, I.; Henderiks, J. Eco-physiological adaptation shapes the response of calcifying algae to nutrient limitation. *Sci. Rep.* **2015**, *5*, 16499. [\[CrossRef\]](#)
- Lazarus, D.; Barron, J.; Renaudie, J.; Diver, P.; Türke, A. Cenozoic planktonic marine diatom diversity and correlation to climate change. *PLoS ONE* **2014**, *9*, e84857. [\[CrossRef\]](#) [\[PubMed\]](#)
- Malinverno, E.; Maffioli, P.; Corselli, C.; De Lange, G.J. Present-day fluxes of coccolithophores and diatoms in the pelagic Ionian Sea. *J. Mar. Syst.* **2014**, *132*, 13–27. [\[CrossRef\]](#)
- Ziveri, P.; Grandi, C.; Stefanetti, A.; Cita, M.B. Biogenic fluxes in Bannock Basin: First results from a sediment trap study (November 1991–May 1992). *Rend. Lincei* **1995**, *6*, 131–145. [\[CrossRef\]](#)
- Malinverno, E.; Ziveri, P.; Corselli, C. Coccolithophorid distribution in the Ionian Sea and its relationship to eastern Mediterranean circulation during late fall to early winter 1997. *J. Geophys. Res. Ocean.* **2003**, *108*, 8115. [\[CrossRef\]](#)
- Stavrakakis, S.; Chronis, G.; Tselepidis, A.; Heussner, S.; Monaco, A.; Abassi, A. Downward fluxes of settling particles in the deep Cretan Sea (NE Mediterranean). *Prog. Oceanogr.* **2000**, *46*, 217–240. [\[CrossRef\]](#)
- Stavrakakis, S.; Gogou, A.; Krasakopoulou, E.; Karageorgis, A.P.; Kontoyiannis, H.; Rousakis, G.; Velaoras, D.; Perivoliotis, L.; Kambouri, G.; Stavrakaki, I.; et al. Downward fluxes of sinking particulate matter in the deep Ionian Sea (NESTOR site), eastern Mediterranean: Seasonal and interannual variability. *Biogeosciences* **2013**, *10*, 7235–7254. [\[CrossRef\]](#)
- Skampa, E.; Triantaphyllou, M.V.; Dimiza, M.D.; Gogou, A.; Malinverno, E.; Stavrakakis, S.; Parinos, C.; Panagiotopoulos, I.P.; Tselenti, D.; Archontikis, O.; et al. Coccolithophore export in three deep-sea sites of the Aegean and Ionian Seas (Eastern Mediterranean): Biogeographical patterns and biogenic carbonate fluxes. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2020**, *171*, 104690. [\[CrossRef\]](#)
- Ziveri, P.; Rutten, A.; De Lange, G.J.; Thomson, J.; Corselli, C. Present-day coccolith fluxes recorded in central eastern Mediterranean sediment traps and surface sediments. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2000**, *158*, 175–195. [\[CrossRef\]](#)

15. Triantaphyllou, M.V.; Ziveri, P.; Tselepidis, A. Coccolithophore export production and response to seasonal surface water variability in the oligotrophic Cretan Sea (NE Mediterranean). *Micropaleontology* **2004**, *50* (Suppl. S1), 127–144. [\[CrossRef\]](#)
16. Malinverno, E.; Triantaphyllou, M.V.; Stavrakakis, S.; Ziveri, P.; Lykousis, V. Seasonal and spatial variability of coccolithophore export production at the South-Western margin of Crete (Eastern Mediterranean). *Mar. Micropaleontol.* **2009**, *71*, 131–147. [\[CrossRef\]](#)
17. Dimiza, M.D.; Triantaphyllou, M.V.; Dermitzakis, M.D. Seasonality and ecology of living coccolithophores in Eastern Mediterranean coastal environment (Andros Island, Middle Aegean Sea). *Micropaleontology* **2008**, *54*, 159–175. [\[CrossRef\]](#)
18. Dimiza, M.D.; Triantaphyllou, M.V.; Malinverno, E.; Psarra, S.; Karatsolis, B.T.; Mara, P.; Lagaria, A.; Gogou, A. The composition and distribution of living coccolithophores in the Aegean Sea (NE Mediterranean). *Micropaleontology* **2015**, *61*, 521–540. [\[CrossRef\]](#)
19. El Hourany, R.; Abboud-abi Saab, M.; Faour, G.; Mejia, C.; Crépon, M.; Thiria, S. Phytoplankton diversity in the Mediterranean Sea from satellite data using self-organizing maps. *J. Geophys. Res. Ocean.* **2019**, *124*, 5827–5843. [\[CrossRef\]](#)
20. Trimonis, E.; Rudenko, M. Geomorphology and bottom sediments of the Pylos area. In Proceedings of the 2nd NESTOR International Workshop; Resvanis, L.K., Ed.; Fortress of Niokastro: Pylos, Greece, 1992; p. 321.
21. D’Ortenzio, F.; Ragni, M.; Marullo, S.; Ribera d’Alcalà, M. Did biological activity in the Ionian Sea change after the Eastern Mediterranean Transient? Results from the analysis of remote sensing observations. *J. Geophys. Res. Ocean.* **2003**, *108*, 8113. [\[CrossRef\]](#)
22. Crombet, Y.; Leblanc, K.; Queguiner, B.; Moutin, T.; Rimmelin, P.; Ras, J.; Claustre, H.; Leblond, N.; Oriol, L.; Pujo-Pay, M. Deep silicon maxima in the stratified oligotrophic Mediterranean Sea. *Biogeosciences* **2011**, *8*, 459–475. [\[CrossRef\]](#)
23. Karageorgis, A.P.; Georgopoulos, D.; Kanellopoulos, T.D.; Mikkelsen, O.A.; Pagou, K.; Kontoyiannis, H.; Pavlidou, A.; Anagnostou, C. Spatial and seasonal variability of particulate matter optical and size properties in the Eastern Mediterranean Sea. *J. Mar. Syst.* **2012**, *105*, 123–134. [\[CrossRef\]](#)
24. Theodosi, C.; Markaki, Z.; Pantazoglou, F.; Tselepidis, A.; Mihalopoulos, N. Chemical composition of downward fluxes in the Cretan Sea (Eastern Mediterranean) and possible link to atmospheric deposition: A 7 year survey. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2019**, *164*, 89–99. [\[CrossRef\]](#)
25. Rutten, A.; De Lange, G.J.; Ziveri, P.; Thomson, J.; Van Santvoort, P.J.M.; Colley, S.; Corselli, C. Recent terrestrial and carbonate fluxes in the pelagic eastern Mediterranean; a comparison between sediment trap and surface sediment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2000**, *158*, 197–213. [\[CrossRef\]](#)
26. Tanaka, T.; Zohary, T.; Krom, M.D.; Law, C.S.; Pitta, P.; Psarra, S.; Rassoulzadegan, F.; Thingstad, T.F.; Tselepidis, A.; Woodward, E.M.S.; et al. Microbial community structure and function in the Levantine Basin of the eastern Mediterranean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2007**, *54*, 1721–1743. [\[CrossRef\]](#)
27. Powley, H.R.; Van Cappellen, P.; Krom, M.D. Nutrient cycling in the Mediterranean Sea: The key to understanding how the unique marine ecosystem functions and responds to anthropogenic pressures. In *Mediterranean Identities—Environment, Society, Culture*; Soc Cult. InTech: London, UK, 2017; pp. 47–77. [\[CrossRef\]](#)
28. Casotti, R.; Landolfi, A.; Brunet, C.; d’Ortenzio, F.; Mangoni, O.; Ribera d’Alcalà, M.; Denis, M. Composition and dynamics of the phytoplankton of the Ionian Sea (eastern Mediterranean). *J. Geophys. Res. Oceans* **2003**, *108*. [\[CrossRef\]](#)
29. Nittis, K.; Pinardi, N.; Lascaratos, A. Characteristics of the summer 1987 flow field in the Ionian Sea. *J. Geophys. Res. Ocean.* **1993**, *98*, 10171–10184. [\[CrossRef\]](#)
30. Malanotte-Rizzoli, P.; Manca, B.B.; d’Alcalà, M.R.; Theocharis, A.; Bergamasco, A.; Bregant, D.; Budillon, G.; Civitarese, G.; Georgopoulos, D.; Michelato, A.; et al. A synthesis of the Ionian Sea hydrography, circulation and water mass pathways during POEM-Phase I. *Prog. Oceanogr.* **1997**, *39*, 153–204. [\[CrossRef\]](#)
31. Estournel, C.; Marsaleix, P.; Ulses, C. A new assessment of the circulation of Atlantic and Intermediate Waters in the Eastern Mediterranean. *Prog. Oceanogr.* **2021**, *198*, 102673. [\[CrossRef\]](#)
32. Larnicol, G.; Ayoub, N.; Le Traon, P.Y. Major changes in Mediterranean Sea level variability from 7 years of TOPEX/Poseidon and ERS-1/2 data. *J. Mar. Syst.* **2002**, *33*, 63–89. [\[CrossRef\]](#)
33. Acker, J.G.; Leptoukh, G. Online analysis enhances use of NASA earth science data. *Eos Trans. AGU* **2007**, *88*, 14–17. [\[CrossRef\]](#)
34. Ziveri, P.; Young, J.R.; Van Hinte, J.E. Coccolithophore export production and accumulation rates. *GeoResearch Forum* **1999**, *5*, 41–56.
35. D’Ortenzio, F.; Ribera d’Alcalà, M. On the trophic regimes of the Mediterranean Sea: A satellite analysis. *Biogeosciences* **2009**, *6*, 139–148. [\[CrossRef\]](#)
36. Patara, L.; Pinardi, N.; Corselli, C.; Malinverno, E.; Tonani, M.; Santoleri, R.; Masina, S. Particle fluxes in the deep Eastern Mediterranean basins: The role of ocean vertical velocities. *Biogeosciences* **2009**, *6*, 333–348. [\[CrossRef\]](#)
37. Gogou, A.; Stavrakakis, S.; Triantaphyllou, M.; Paraskos, F.; Parinos, C.; Dimiza, M.; Kambouri, G.; Lykousis, V. Seasonal and interannual variability of sinking particulate matter in the deep Ionian Sea: Ecological and biogeochemical perspectives. *Rapp. Comm. Int. Mer Médit.* **2016**, *41*. Available online: https://ciesm.org/online/archives/abstracts/pdf/41/CIESM_Congress_2016_Kiel_article_0083.pdf (accessed on 11 October 2022).
38. Turner, J.T. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* **2002**, *27*, 57–102. [\[CrossRef\]](#)

39. Schulz, M.; Prospero, J.M.; Baker, A.R.; Dentener, F.; Ickes, L.; Liss, P.S.; Mahowald, N.M.; Nickovic, S.; García-Pando, C.P.; Rodríguez, S.; et al. Atmospheric transport and deposition of mineral dust to the ocean: Implications for research needs. *Environ. Sci. Technol.* **2012**, *46*, 10390–10404. [\[CrossRef\]](#)
40. Cascella, A.; Bonomo, S.; Jalali, B.; Sicre, M.A.; Pelosi, N.; Schmidt, S.; Lirer, F. Climate variability of the last ~2700 years in the Southern Adriatic Sea: Coccolithophore evidence. *Holocene* **2020**, *30*, 53–64. [\[CrossRef\]](#)
41. Molinaroli, E.; Guerzoni, S.; Rampazzo, G. Contribution of Saharan dust to the Central Mediterranean Basin. *Geol. Soc. Am. Spec. Pap.* **1993**, *284*, 303–312. [\[CrossRef\]](#)
42. Klaas, C.; Archer, D.E. Association of sinking organic matter with various types of mineral ballast in the deep sea: Implications for the rain ratio. *Glob. Biogeochem. Cycles* **2002**, *16*, 63–1. [\[CrossRef\]](#)
43. Young, J.R. Variation in *Emiliania huxleyi* coccolith morphology in samples from the Norwegian EHUX experiment, 1992. *Sarsia* **1994**, *79*, 417–425. [\[CrossRef\]](#)
44. Molfino, B.; McIntyre, A. Precessional forcing of nutricline dynamics in the equatorial Atlantic. *Science* **1990**, *249*, 766–769. [\[CrossRef\]](#)
45. Triantaphyllou, M.V.; Ziveri, P.; Gogou, A.; Marino, G.; Lykousis, V.; Bouloubassi, I.; Emeis, K.-V.; Kouli, K.; Dimiza, M.; Rosell-Melé, A.; et al. Late Glacial–Holocene climate variability at the south-eastern margin of the Aegean Sea. *Mar. Geol.* **2009**, *266*, 182–197. [\[CrossRef\]](#)
46. Bonomo, S.; Schroeder, K.; Cascella, A.; Alberico, I.; Lirer, F. Living coccolithophore communities in the central Mediterranean Sea (Summer 2016): Relations between ecology and oceanography. *Mar. Micropaleontol.* **2021**, *165*, 101995. [\[CrossRef\]](#)
47. Kleijne, A. Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton). *Neth. J. Sea Res.* **1993**. Available online: <https://www.amazon.co.uk/Morphology-Distribution-Coccolithophorids-Calcareous-Nannoplankton/dp/9090061614> (accessed on 11 October 2022).
48. Knappertsbusch, M. Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea. *Mar. Micropaleontol.* **1993**, *21*, 219–247. [\[CrossRef\]](#)
49. Flores, J.A.; Sierro, F.J.; Francés, G.; Vázquez, A.; Zamarren, I. The last 100,000 years in the western Mediterranean: Sea surface water and frontal dynamics as revealed by coccolithophores. *Mar. Micropaleontol.* **1997**, *29*, 351–366. [\[CrossRef\]](#)
50. Colmenero-Hidalgo, E.; Flores, J.A.; Sierro, F.J.; Bárcena, M.Á.; Löwemark, L.; Schönfeld, J.; Grimalt, J.O. Ocean surface water response to short-term climate changes revealed by coccolithophores from the Gulf of Cadiz (NE Atlantic) and Alboran Sea (W Mediterranean). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2004**, *205*, 317–336. [\[CrossRef\]](#)
51. Dimiza, M.D.; Triantaphyllou, M.V.; Malinverno, E. New Evidence for The Ecology of *Helicosphaera Carteri* In Polluted Coastal Environments (Elefsis Bay, Saronikos Gulf, Greece). *JNR* **2014**, *34*, 37–43.
52. Boeckel, B.; Baumann, K.-H. Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean. *Mar. Micropaleontol.* **2008**, *67*, 255–273. [\[CrossRef\]](#)